

# A revised synonymy of the minnow genus *Phoxinus* Rafinesque, 1820 (Teleostei: Cyprinidae) with comments on its relationships and distribution

Gordon J. Howes

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

## Introduction

*Communication between scientists and the public will not be aided or enhanced by the overeager adoption of new names until the old ones have been shown to be inadequate.* So comment Scott & Crossmann (1973) in response to the acceptance by some recent authors of Bănărescu's (1964) synonymy of the nearctic minnow genus *Chrosomus* with the palearctic *Phoxinus*. This particular case has highlighted the confusion of supra-specific cyprinid taxonomy and the fact that rigorous definitions of most cyprinid taxa just do not exist. Previous work has failed to make direct anatomical comparisons of the various genera and 'generic characters' have included morphometric and meristic variables such as body depth, number of lateral line scales, degree of completeness of the lateral-line, and peritoneal pigmentation. At best, such characters indicate specific, populational or individual differences. The inadequacy of such 'generic characters' is particularly evident when attempting to discriminate between so-called phoxinine genera; *i.e.* *Phoxinus*, *Phoxinellus* and *Pseudophoxinus* (see, for example, the remarks in Coad, 1981).

This review of the synonymy of *Phoxinus* has been initiated through a wider study embracing the phyletic classification of all Old-World leuciscine cyprinids. In the course of renewed efforts to identify a sister-group of the aspinine assemblage (*sensu* Howes, 1978) it became evident that a group of taxa including *Phoxinus* possessed a suite of synapomorphies. It was also evident that some taxa currently recognised as synonyms of *Phoxinus* are valid genera. A definition of *Phoxinus* is presented here with a critique of former synonymies, together with a revised synonymy. In addition notes are included on the possible relationships of *Phoxinus*, and, in the light of the revised synonymy, the geographical distribution of the genus.

## List of study material

Abbreviations: AMNH, American Museum of Natural History; BMNH, British Museum (Natural History); CAS, Californian Academy of Sciences; FMNS, Field Museum of Natural History; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum.

The taxonomic and anatomical descriptions in this paper are based on the following specimens. In addition, material listed in Howes (1978) was used for out-group comparisons.

*Achahara semotilus*, syntypes, USNM 45227.

*Coesius plumbeus*, BMNH 1893.2.7:637-645; 1935.4.21:2-5; UMMZ 133303; 145587.

*Eupallasella percunus*. BMNH 1893.1.27:14-17; 1895.10.14:70-73; 1925.8.6:24; *E. percunus stagnalis* 1899.7.25:36.

*Hybognathus hankinsoni*, BMNH 1973.2.3:48-57.

*Lagowskiella lagowskii*, BMNH 1974.8.6:21-30; 1923.8.6:23; USNM 76732; 76726; 76722; 82303; 48937; 105173; 105215.

*Oreoleuciscus humilis*, BMNH 1974.8.6:63-72.

'*Phoxinellus*' *callensis*, BMNH 1912.5.29:1-7.

'*Phoxinellus*' *epiroticus*, BMNH 1979.2.21:161.

'*Phoxinellus*' *ghetaldii*, BMNH 1903.12.4:37-40.

'*Phoxinellus*' *pstrossi*, BMNH 1911.9.28:4-5, syntypes.

'*Phoxinellus*' *metohiensis*, BMNH 1911.9.22:12-13, syntypes.

*Phoxinus cumberlandensis*, UMMZ 201152.

*Phoxinus eos*, UMMZ 185407.

*Phoxinus erythrogaster*, BMNH 1972.2.3:11–20; 21–32; 1982.4.13:4311–320; UMMZ 144867.

*Phoxinus neogaeus*, BMNH 1963.10.28:56–60; UMMZ 108044.

*Phoxinus oreas*, BMNH 1983.8.19:33–34.

*Phoxinus phoxinus*, BMNH 1974.8.6:31–42 (Mongolia); 1968.11.5:47–63; 1969.1.24:139–554; 1974.8.6:31–42; 43–62; 1982.11.15:22–33 (all U.K. localities).

'*Phoxinus*' *czekanowskii*, BMNH 1871.7.19:22–23.

'*Phoxinus*' *poljakowi*, BMNH 1849.7.25:34.

*Pseudaspius bergi*, CAS(SU)22393; FMNS 55801 (all syntypes).

*Rhynchocypris costatus* AMNH 10917; 10909; 10914.

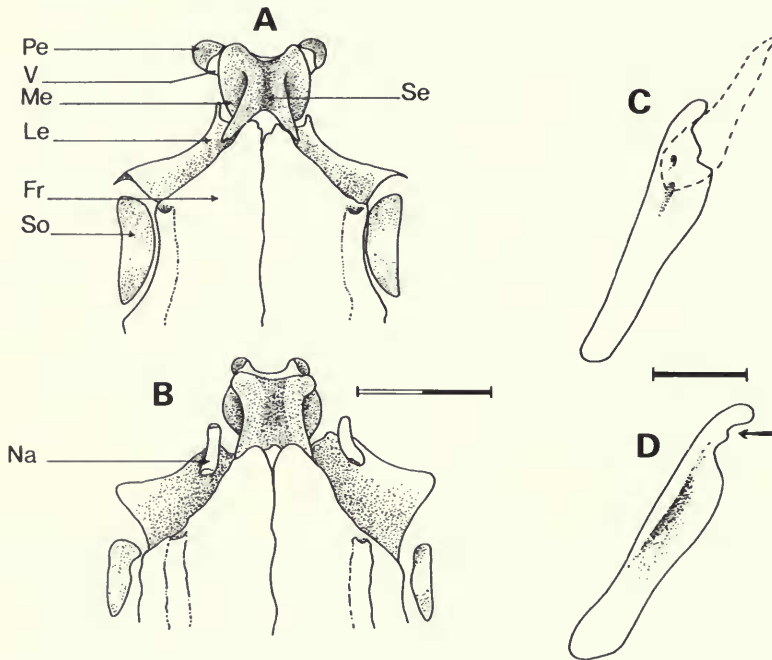
*Rhynchocypris steindachneri* BMNH 1891.10.15; 1907.12.23:11–14; UMMZ 202118.

*Rhynchocypris oxycephalus*, BMNH 1895.5.31:41–43; 1910.6.30:63–64.

*Rhynchocypris variegatus*, BMNH 1889.6.8:97–106 (syntypes)

*Semotilus atromaculatus* BMNH 1982.4.13:4531–40.

*Tribolodon jouyi* USNM45228 (syntypes); BMNH 1907–12.10:57–62.



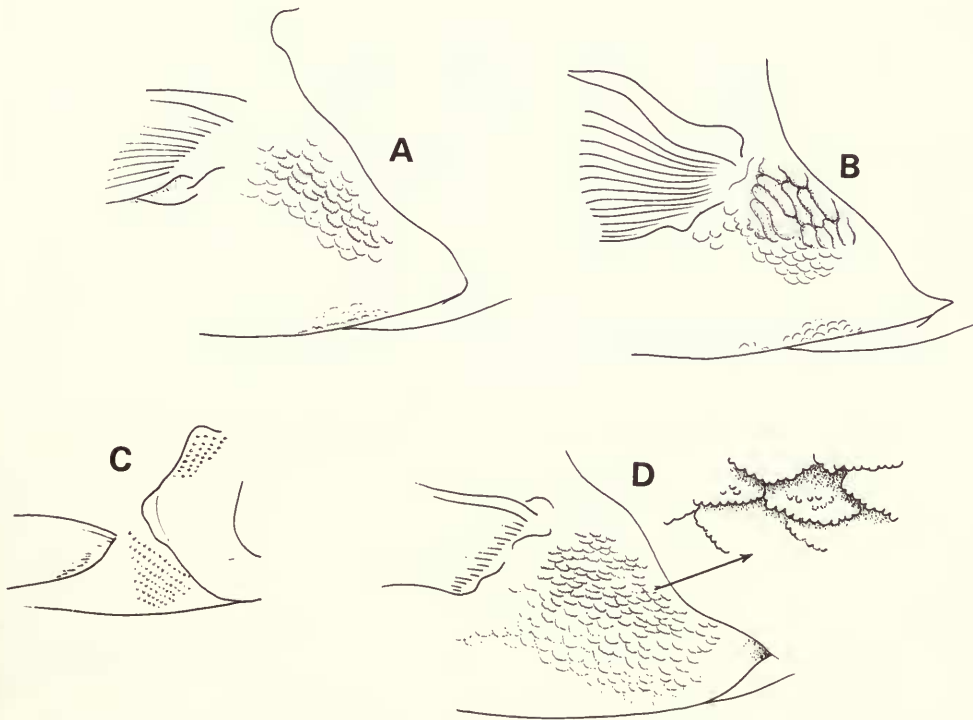
**Fig. 1** Dorsal views of the ethmoid regions of A, *Phoxinus phoxinus*; B, *Ph. erythrogaster*. Supracleithrum of, C, *Ph. phoxinus* in lateral view (dashed line indicates posttemporal); D, *Ph. erythrogaster* in medial view. Arrow indicates dorsal notch. Fr=frontal; Le=lateral ethmoid; Me=mesethmoid; Na=nasal; Pe=preethmoid; Se=supraethmoid; So=supraorbital; V=vomer. Scales in mm.

### Definition of *Phoxinus*

Comparative analysis with a wide range of cyprinid taxa has indicated that the following characters are synapomorphic for the included species: supraethmoid elongate, narrow-waisted; dorsal tip of supraclathrum formed into a notch, the upper part articulating with a medial shelf or process of the posttemporal (Fig. 1C;D); supraorbital minute; nasal reduced (in some individuals of *Phoxinus phoxinus* to an epidermal canal) and widely separated from the anterior frontal canal opening (Fig. 1B); diagonal rows of comb-like scales in the pectoral area which in breeding males are tuberculate (Fig. 2A–C); scales absent from the abdominal region in some species.

**Diagnosis:** Fishes of adult size up to 120 mm SL, body elongate, terete (depth, Mean of included species is 30% of standard length); mouth horizontal or slightly oblique; jaw bones shallow, maxilla slender, spear-shaped; dentary without symphyseal process, coronomeckelian bone (sesamoid articular) well-developed elongate and spear-shaped, often with a broad medial flange; olfactory foramen small, almost entirely within the lateral ethmoid, with, in some species, the upper border of the foramen produced forward as a bony flange; palatine laterally flared; pterosphenoids separated from one another by the optic foramen; infraorbitals reduced; dermosphenotic present; subtemporal fossa small, ovate or ellipsoidal and often with an anterior extension into the pterotic, roofed mainly by the epioccipital (Fig. 3A); posttemporal fossa absent; supraoccipital crest absent; no connection between the preopercular and supraorbital sensory canals; intercalar well-developed, sometimes with a posterior process; coracoid strut-like; symphysis of the cleithrum club-shaped; scales usually small, 60 to more than 90 in the lateral-line; olfactory lamellae finger-like, 20–30; gill-rakers few, 5–10 (rarely 11 or 12) on 1st ceratobranchial; anterior part of 1st ceratobranchial covered by epithelial tissue sealing it closely to the hyoid bar, leaving only a small gap between the bucco-pharyngeal and opercular cavities; shallow neural complex on 3rd vertebrae; 2 or 3 feebly developed anterior supraneurals; mean number of vertebrae (for all species) 38; marked sexual dimorphism expressed in breeding coloration and the diagonal rows of modified, comb-like scales on the pectoral regions of ripe males and females (Fig. 2); lips often highly papillose and buccal roof tissue furrowed and tuberculate (Figs 7A–E).

In view of the above re-definition, the currently accepted concept of *Phoxinus* requires revision. This concept has been based principally on the works of Berg and Bănărescu.



**Fig. 2** Pectoral squamation in ripe males (comb-scales) of A, *Phoxinus phoxinus* BMNH 1968.11.5: 47–63, 55.5 mm SL; B, *Ph. neogaeus* BMNH 1963.10.28: 56–60, 68.5 mm SL; C, *Ph. erythrogaster* UMMZ 144867, 42.5 mm SL, also showing 'prickles' on operculum; D, *Couesius plumbeus* BMNH 1935.4.21: 2–5, 84 mm SL, with some scales magnified to 50 × .

### Critique of generic synonymies of Berg and Bănărescu

#### *Berg's synonymies*

The synonymy given by Berg (1949) is with some additions, basically that published in 1912, and has been widely accepted. Its acceptance has, however, been uncritical and a close analysis of the included taxa leads to substantial modification.

Berg listed as synonyms of *Phoxinus* the following: *Gila* Baird & Girard, 1854; *Rhynchocypris* Günther, 1889; *Eulinneela* Dybowski, 1916; *Lagowskiella* Dybowski, 1916; *Eupsallasella* Dybowski, 1916; *Czekanowskiella* Dybowski, 1916; *Pfrille* Jordan, 1924 and *Moroco* Jordan & Hubbs, 1925.

Of his two included nearctic genera, *Gila* is recognised as a distinct taxon (see Miller, 1945) and *Pfrille* is generally regarded as a synonym of *Chrosomus* (see discussion and synonymy below, and Scott & Crossmann, 1973: 397).

Of the other included taxa, *Eulinneela* is here accepted as a synonym of *Phoxinus* (see p. 66) but *Rhynchocypris*, *Eupallasella*, *Lagowskiella*, *Czekanowskiella* and *Moroco* are not. Reasons for their exclusion from synonymy and their recognition as distinct taxa are as follows:

#### **RHYNCHOCYPRIS** Günther, 1889

TYPE SPECIES: *Rhynchocypris variegatus* Günther, 1889 (= *Pseudophoxinus oxycephalus* Sauvage & Dabry, 1874).

This is a distinctive taxon characterised by the following apomorphies: fleshy rostral process, most highly developed in ripe females (Fig. 4), hypertrophied olfactory lamellae with crenate ventral margins; attenuated posterior border of the operculum and a distinct notch in the dorsal border of the upright part of the cleithral lamellae.

Berg (1912) recognised, correctly, that *Rhynchocypris variegatus* Günther, 1889 was a synonym of *Pseudophoxinus oxycephalus* Sauvage & Dabry, 1874. However, he also recognised *oxycephalus* as a subspecies of *Phoxinus lagowskii* Dybowski, 1869. This is incorrect, since *Phoxinus lagowskii* represents a taxon quite distinct from *Rhynchocypris oxycephalus* (see p. 63).

*Rhynchocypris oxycephalus* has been disregarded by many authors and appears in the literature under the following erroneous combinations: *Leuciscus brandti* Fowler, 1899; 1924; *Phoxinus percunurus sachaliensis* Berg, 1906; *Phoxinus lagowskii variegatus* Berg, 1912; *Pseudaspius modestus* Jordan & Metz, 1913; *Ph. lagowskii chorensis* Rendahl, 1928; *Moroco variegatus* Mori, 1930; *Moroco variegatus septentrionalis* Mori, 1930; *Moroco oxycephalus* Mori, 1930; *Ph. lagowskii variegatus*, Berg, 1932; *Ph. lagowskii oxycephalus* Berg, 1932; 1949 (part; Takema River).

Two other species of *Rhynchocypris* are recognised here; *R. steindachneri* (Sauvage, 1883) and *R. costatus* (Fowler, 1899). Both species differ from *R. oxycephalus* in being shallower bodied and in having fewer gill-rakers on the 1st ceratobranchial and a different body colour-pattern (Fig. 5B).

*Rhynchocypris steindachneri* has a shorter head than that of *R. oxycephalus* and modally shorter than that of *R. costatus*; it also has a greater interorbital width than the two latter species; see Table I. The lateral line scale count in *R. steindachneri* is less than in *R. oxycephalus* (80–88) and *R. costatus* (80–84). Characteristic body markings of *R. steindachneri* comprise dark mottling overlying a deep lateral band; the head and snout are dark (Fig. 5A).

The following synonyms are those recognised by Okada (1960) under *Moroco steindachneri*: *Phoxinus steindachneri* Sauvage, 1883; *Hemitremia steindachneri*, Jordan, Tanaka & Snyder, 1913; *Leuciscus steindachneri*, Jordan & Snyder, 1901; *Leuciscus dorobae* Ishikawa, 1904; *Pseudaspius atrilatus* Jordan & Thompson, 1914; *Moroco steindachneri*, Jordan & Hubbs, 1925; Okada, 1960; *Moroco yamamotis* Jordan & Hubbs, 1925.

*Rhynchocypris costatus* is immediately distinguished from its congeners by its elongate body, longer operculum and high vertebral number (see Table 1). The body markings show less mottling than in *R. oxycephalus* and there is a deeper lateral band than in *R. steindachneri* (Fig. 5c).

Since it was originally described by Fowler (1899) as *Leuciscus costatus*, the species has been recognised as a synonym of *Phoxinus lagowskii oxcephalus* by Fowler (1924), Mori (1934), Berg (1912:1949) and by Nichols (1928). Mori (1934 : 24–27) described both *Phoxinus oxycephalus* and *Ph. lagowskii* from Jehol (N.E. China). However, his figures of these species (Pl.X, figs 1 & 2) depict, respectively, female and male specimens of *R. costatus*. The *Ph. lagowskii oxycephalus* from Suifin reported by Dulckeit (1927) is also possibly *R. costatus*.

Although all the American Museum specimens are labelled as *Rhynchocypris costatus* (apparently by Nichols), this combination does not appear to have been published, and to my knowledge is done so here for the first time.

**Table 1** Morphometric and meristic comparisons between *Rhynchocypris* species

	<i>oxycephalus</i>		<i>steindachneri</i>		<i>costatus</i>	
	Range	M	Range	M	Range	M
	(10 specimens, 81–105 mm SL)		(5 specimens, 76.5–87.3 mm SL)		(25 specimens, 51–135 mm SL)	
% of SL:						
D	20.7–24.0	22.5	20.0–23.2	21.8	16.6–21.5	17.1
H	26.0–28.0	26.8	22.8–25.9	25.1	23.2–29.4	26.9
D–S	53.8–56.7	55.3	53.9–56.7	50.7	48.5–57.0	53.2
CpL	20.5–24.0	22.7	23.4–25.1	23.9	20.7–29.6	24.2
CpD as % of its length:						
	48.0–61.0	52.4	45.0–50.0	48.8	31.4–48.9	43.5
% of head length:						
IO	28.0–35.2	31.7	32.4–36.3	34.5	26.9–32.8	29.4
Sn	28.6–35.2	31.0	29.5–33.0	31.2	25.0–32.7	29.6
Eye	16.4–21.5	19.7	21.0–24.3	22.6	19.2–26.5	23.0
GR	1–2/5–7		2/4–5		2–3/4–5	
Ll	80–88		70–80		80–84	
Vertebrae	36 total (4+17–18+1)		37–38 (4+17–18+19+1)		42–44 (4+19–20+18–20+1)	

D = body depth; H = head length (not including rostral process); D–S = distance between snout and 1st dorsal fin ray; CpL, CpD = caudal peduncle length and depth; IO = interorbital width; Sn = snout length (not including rostral process); Eye = eye diameter; GR = gill-rakers on epibranchial/ceratobranchial; Ll = lateral line scales. Vertebral counts are the 4 Weberian vertebrae, abdominal, caudal and fused preural–ural centrum.

### *EUPALLASELLA* Dybowski, 1916

TYPE SPECIES: *Cyprinus percunurus* Pallas, 1811.

Dybowski (1916) recognised the distinctiveness of *Phoxinus percunurus* by placing it in a separate genus, *Eupallasella* but Berg (1912; 1949) treats this taxon as a synonym of *Phoxinus*.

Gasowska (1979) made an osteological comparison of *Ph. percunurus* and *Ph. phoxinus*, concluding that *Ph. percunurus* was distinct enough to warrant its assignment to a separate genus. In her opinion, *Ph. percunurus* was closely related to *Rhynchocypris oxycephalus*. However, her uncritical acceptance of Berg's synonymy of *R. oxycephalus* with *Moroco bergi* (Jordan & Metz, 1913) caused her to refer *percunurus* to the genus *Moroco*. In fact, *Moroco* is a synonym of *Lagowskiella* (see p. 63 below) and *Ph. percunurus* shares none of those characters which define that genus.

Of the osteological characters differentiating *Ph. percnurus* from *Ph. phoxinus* listed by Gasowska (1979), those for *percnurus* appear to be plesiomorphic (*i.e.* broad supraethmoid and supraorbital; pentagonal 1st infraorbital; shallow urohyal median plate; symmetrical neural complex; short operculum with rounded border). Of the other morphological characters which Gasowska lists, the mouth shape is significantly different. In *Ph. phoxinus* the mouth is subterminal, almost horizontal and with the lower jaw articulation beneath the anterior margin of the orbit. In *Ph. percnurus* the mouth is terminal, the lower jaw obliquely aligned with its articulation anterior to the orbital border, (Fig. 6).

*Phoxinus percnurus* lacks the characteristic pectoral 'comb scales' and naked abdomen of *Phoxinus (sensu stricto)* and also lacks those synapomorphies characterising the other genera considered here although the presence of an interpelvic flap, strongly imbricate scales and a mottled body pattern are characteristics shared with *Rhynchocypris*. *Phoxinus percnurus* has, however, a significantly greater body depth than any *Rhynchocypris* species or *Phoxinus* species, it being 25.9–29.4% of SL (*cf.* Table 1). There are also a higher number of gill-rakers in *percnurus* (8–9 on the 1st ceratobranchial) than in *Rhynchocypris* and the Eurasian *Phoxinus* species (*phoxinus; brachyurus*).

Since certain osteological and other morphological characters exclude *percnurus* from both *Phoxinus* and *Rhynchocypris* (see above) I refer the species to its former genus, *Eupallasella*. Berg (1949) lists six subspecies of *E. percnurus*. Of these, the Sakhalin minnow, *percnurus sachaliensis* is referred to *Rhynchocypris oxycephalus* (see p. 60).

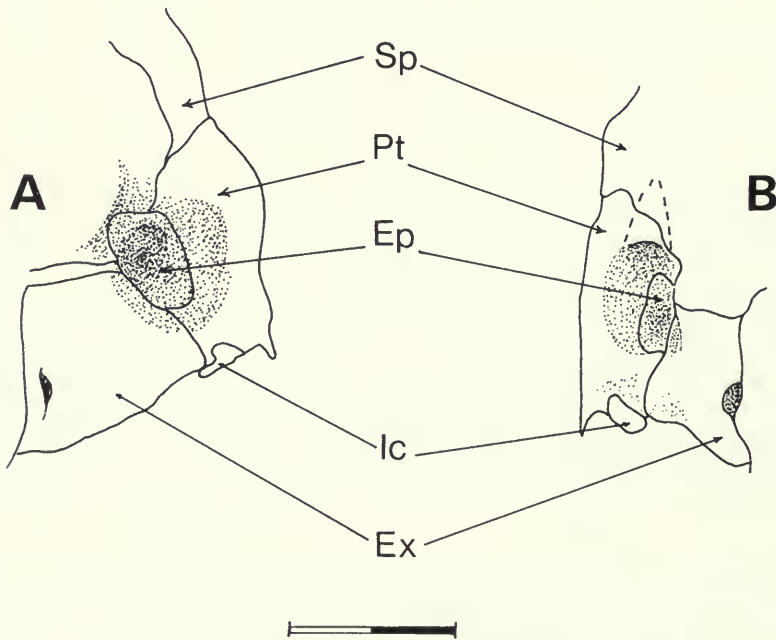


Fig. 3 Subtemporal fossae of A. *Phoxinus phoxinus* and B. *Lagowskiella lagowskii*. Dashed line indicates anterior chamber of fossa. Ep = epioccipital; Ex = exoccipital, Ic = intercalar; Pt = pterotic; Sp = sphenotic. Scale in mm.

#### MOROCCO Jordan & Hubbs, 1925

TYPE SPECIES: *Pseudaspius bergi* Jordan & Metz, 1913 (= *Phoxinus lagowskii* Dybowski, 1869).

Having examined syntypes of *Pseudaspius bergi* (CAS(SU)22393, 92 mm SL and FMNS 55801, 59 & 61 mm SL, all from Chinnampo, Korea), I agree with Berg (1949) that this taxon is a

synonym of *Phoxinus lagowskii* Dybowski, 1869. Although Jordan & Metz (1913) give a lateral line scale count of '... 100', I count 86 scales in the types, cf. 72–87 in *Ph. lagowskii*. Berg is wrong, however, in assigning the species *lagowskii* to *Phoxinus*. This species shares none of the derived characters that define *Phoxinus* species, and differs from those species in the following features:

Character	' <i>Phoxinus</i> ' <i>lagowskii</i>	<i>Phoxinus</i> ( <i>sensu stricto</i> )
Supraethmoid	broad with a V-shaped notch	narrow with a shallow notch
Nasal	elongate	short
Supraorbital	large	minute
Infraorbitals 4 & 5	slightly divergent from orbit	vertical
Dilatator fossa incorporates	sphenotic	pterotic and sphenotic
Orbitosphenoid	elongate, extensive contact with parasphenoid	short, minimal contact with parasphenoid
Operculum	elongate with attenuated lower posterior border	almost square with rounded border
Supracleithrum	elongate, without notch	short, with dorsal notch (Fig. 1c)
Subtemporal fossa	epioccipital reduced, anterior extension into the sphenotic and pterotic (Fig. 3B)	epioccipital forms major part of roof; short anterior extension into the pterotic (Fig. 3A)
Posterior cleithral lamina	short	long
Gill-rakers	thin, with crenate and papillate medial border; 8–9 on ceratobranchial	short and fleshy
Total vertebrae	40–44	36–40

In addition, *lagowskii* has a broader and longer post-orbital cranial region, a more elongate body and posteriorly placed anal fin than any *Phoxinus* species (Fig. 5D). The apomorphic gill-raker morphology, cranial elongation, anterior extent of the subtemporal fossa, attenuated operculum and high vertebral number are features shared with aspinine cyprinids (see Howes, 1978; 1984). Only the lack of a pterosphenoid origin for the *adductor arcus palatini* muscle precludes its inclusion within the aspinine group, and thus it appears as the sister-lineage to that assemblage.

Since it lacks *Phoxinus* synapomorphies and possesses those characters which affiliate it with the aspinines, the species *lagowskii* is referred to the genus *Lagowskiella* Dybowski, 1916, originally established as a subgenus of *Phoxinus* to contain this species. *Moroco* is thus recognised as a junior synonym of *Lagowskiella*; of those species formerly referred to *Moroco*, *steindachneri* Sauvage, 1883 is considered to be a species of *Rhynchocypris* (see above) and *jouyi* Jordan & Snyder, 1901 is recognised as a species of *Tribolodon* due to its ethmoid morphology being synapomorphic with species of that genus. The synonymy of *Lagowskiella* is as follows:

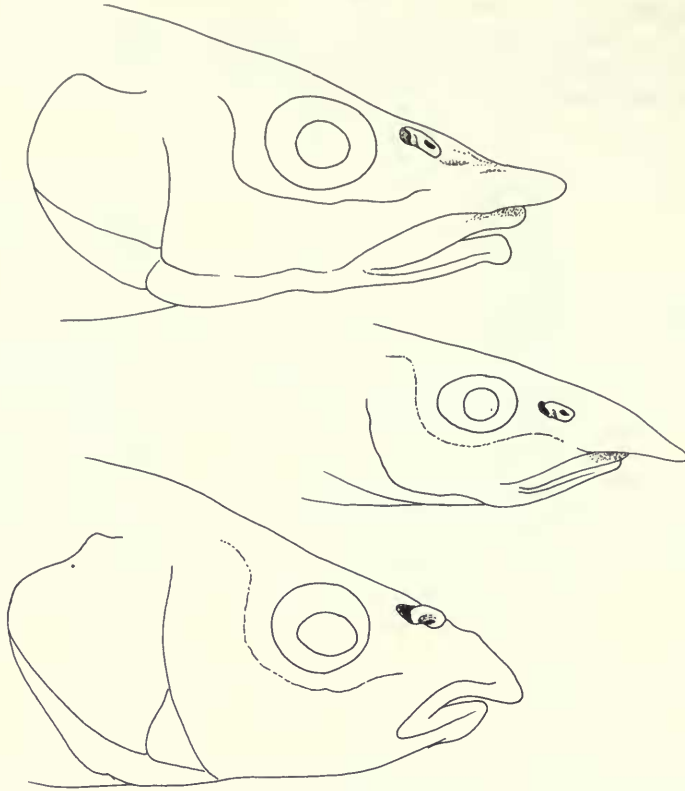
### *LAGOWSKIELLA* Dybowski, 1916

TYPE SPECIES: *Phoxinus lagowskii* Dybowski, 1869.

*Moroco* Jordan & Hubbs, 1925 (type *Pseudaspius bergi* Jordan & Metz, 1913)

?*Czekanowskiella* Dybowski, 1916 (subgenus of *Phoxinus*; type: *Ph. czekanowskii* Dybowski, 1869).

*Lagowskiella lagowskii* is distributed in the Amur, basin of the Lena, basins of Lake Khanka, Ussuri, Khor, Sungari and in Korea. The citations to *Phoxinus lagowskii* given in Berg (1949) and that listed in Berg (1909, Fishes of the Amur) are taken to refer to this species. The *Phoxinus lagowski* (sic) subspecies of Mori (1928) from the Yalu river, Korea is possibly also this species. *Phoxinus poljakowi*, *Ph. czekanowskii*, *Ph. dementjevi* and *Ph. grumi* should probably also be referred to *Lagowskiella* (see p. 67 below).



**Fig. 4** Head profiles, showing rostral extension of, above, *Rhynchocypris oxycephalus* (syntype of *R. variegatus*) BMNH 1889.6.8: 97–100, 108 mm SL: centre, *R. steindachneri*, ripe female, UMMZ 202118, 83 mm SL: below, '*Phoxinellus*' *pstrossi*, female BMNH 1911.9.28: 4–5, 87 mm SL.

#### *Bănărescu's synonymy*

Bănărescu (1964) followed Berg's (1949) synonymy of *Phoxinus* although he omitted *Gila* (which he recognised as a subgenus of *Leuciscus*) and Dybowski's various taxa. Bănărescu recognised *Chrosomus* as a subgenus of *Phoxinus*, thus admitting, as a consequence, four nearctic species to *Phoxinus*, viz: *neogaeus*, *oreas*, *erythrogaster* and *eos*. Two others were added subsequently *Ph. margarita* (Cope, 1868) by Legendre (1970) and *Ph. cumberlandensis* by Starnes & Starnes (1978); see below, p. 68.

Bănărescu's synonymisation of *Chrosomus* and *Phoxinus* has evoked varying responses, with acceptance, or partial acceptance by some authors (Bailey *et al.*, 1970; McPhail & Lindsey, 1970; Legendre, 1970; Starnes & Starnes, 1978) and rejection by others (Scott & Crossmann, 1973, see quotation above, p. 57; Gasowska, 1979; Howes, 1981).

Detailed studies of the comparative osteology of *Phoxinus* and *Chrosomus* have been published respectively by Mahy (1975) and Gasowska (1979), Mahy's work demonstrated minimal differences between species of the two genera and supported Bănărescu's synonymy. Mahy maintained that *Chrosomus neogaeus* was more closely related to *Phoxinus phoxinus* than to other *Chrosomus* species. Gasowska rejected the synonymy of Bănărescu and claimed to show marked osteological differences between *Phoxinus* and *Chrosomus*. Taking a step even further, Gasowska introduced the genus *Parchrosomus* for the species *Chrosomus oreas*. Her recognition of genera, however, is dependent mainly upon differences in the shape of the basioccipital pharyngeal process. Such variability in the process is well within that of other cyprinid genera (pers. obs.) and cannot, on its



own, be used as a 'generic' character. Gasowska does not assign any polarity to the osteological differences she recognises, and ultimately separated the genera largely on alimentary canal length and body coloration. Although Gasowska points out the apomorphic nature of the pectoral squamation in *Ph. phoxinus*, she does not recognise its presence in 'Chrosomus' species.

Howes (1981) opined that *Phoxinus* and *Chrosomus* were distinct genera, on the basis of what was regarded as a synapomorphic neural complex in *Chrosomus* species. Further examination of the osteology of several *Phoxinus* species reveals that this character is variable within the framework of other synapomorphies (see p. 58). Thus, on derived osteological and other characters there is no reason to maintain the separation of *Phoxinus* and *Chrosomus*.

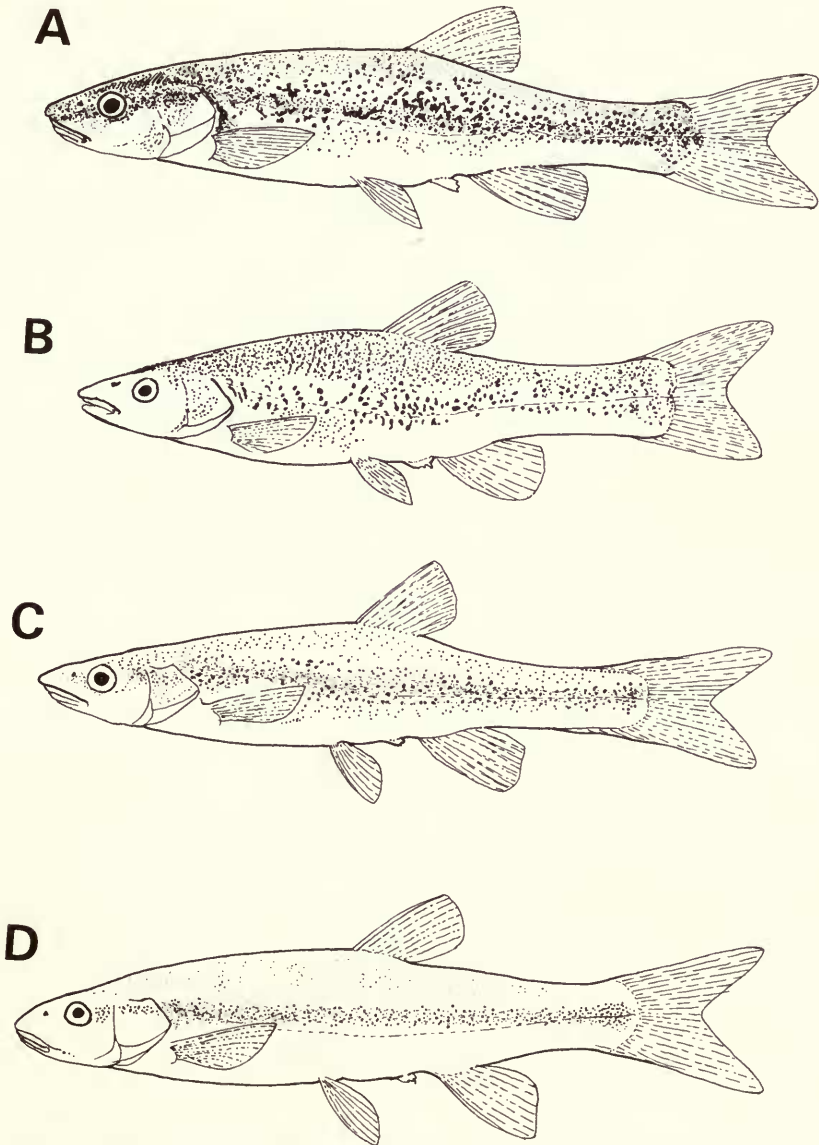


Fig. 5 Outline drawings showing pigment patterns in A, *Rhynchocypris steindachneri*; B, *R. oxycephalus*; C, *R. costatus*; D, *Lagowskiella lagowskii*.

A revised synonymy of *Phoxinus***PHOXINUS** Rafinesque, 1820

TYPE SPECIES: *Cyprinus phoxinus* Linnaeus, 1758, *Syst. Nat.* 10th ed.: 322 (Europe).

*Chrosomus* Rafinesque, 1820, *Ichthyologia Ohiensis*: 47 (type species: *C. erythrogaster* Raf., 1820)

*Eulinneella* Dybowski, 1916, *Pamiętn. Fizjograf.* **23**: 101 (subgenus, type species: *Ph. phoxinus* Linn.)

*Pfifille* Jordan, 1924, *Copeia*, **1924**: 71 (type species: *Ph. neogaeus* Cope, 1869)

?*Achahara* (Jordan & Hubbs, 1925, *Mem. Carnegie Museum* **10** (2): 177 (type species: *Richardsonius semotilus* Jordan & Starks, 1905)

*Parchrosomus* Gasowska, 1979. *Annales zoologici Warszawa* **34** (12): 404 (type species: *Chrosomus oreas* Cope, 1868)

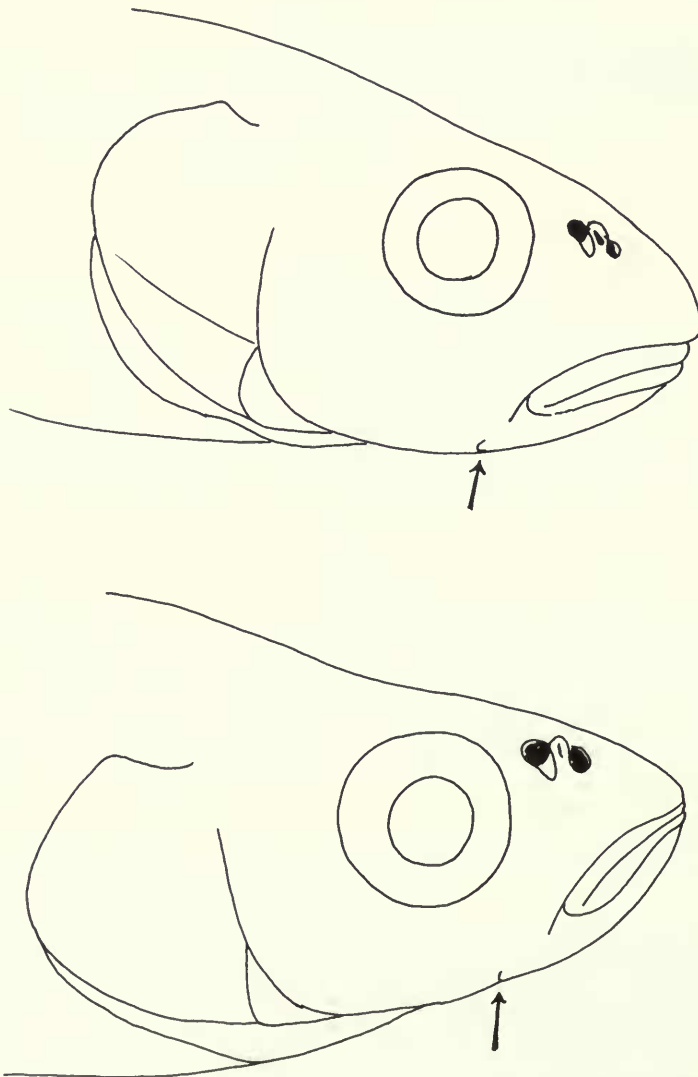


Fig. 6 Head profiles showing mouth-jaw position in, above, *Phoxinus phoxinus* BMNH 1969.1.24: 139-554, 55.5 mm SL; below, *Eupallasella percunurus* BMNH 1925.8.6: 24, 75 mm SL. Arrows indicate lower jaw articulation.

### Notes on this synonymy

The reasons for including *Chrosomus* with *Phoxinus* have been discussed above (p. 64); *Pfrille* is a junior synonym of *Chrosomus* and thus of *Phoxinus*.

*Achahara* was first used as a generic name by Mori (1930) and derived from the manuscript label of Jordan & Hubbs. Mori did not offer a diagnosis of the genus but referred to it the species *Richardsonius semotilus* Jordan & Starks, 1905, and *Telestes brandti* Dybowski, 1872. When Jordan & Hubbs (1925) defined *Achahara* they chose *Richardsonius semotilus* as the type species to conform with Mori's previous orthotypy. Their description of the genus appears, however, to be based not on the species *semotilus* but on *Telestes brandti*, now generally regarded as belonging to the genus *Tribolodon*.

Ikeda (1938) first considered *Achahara semotilus* to be a synonym of *Tribolodon brandti*, believing that Jordan & Stark's specimens were juveniles of that species. Ikeda's synonymy was followed by Berg (1949) and Okada (1960), although Lindberg & Legeza (1965) regard *Achahara* as a synonym of *Leuciscus*. These synonymies are, however, erroneous because *Achahara semotilus* possesses features which are quite distinct from those of any *Tribolodon* or *Leuciscus* species. In the syntypes of *Achahara semotilus* (USNM 45227, 66–190 mm SL), the bucco-pharyngeal and opercular cavities communicate through only a small opening, and there are only 2–3 gill-rakers on the 1st ceratobranchial (cf. extensive bucco-branchial gap, and 13–21 gill-rakers in *Tribolodon*). The rakers also lack the crenate and papillate margin characteristic of *Tribolodon* (Howes, 1984). No osteological material is available for *Achahara* so it cannot be determined whether phoxinine skeletal synapomorphies are present. Neither is it known if comb-like breast scales are present in ripe males. In the morphology of the branchial arches and in their overall appearance, *Achahara semotilus* resembles species of *Phoxinus* more closely than those of any other genus. Until more material is available for detailed investigation, *Achahara* is questionably referred to the synonymy of *Phoxinus*.

Robins *et al.* (1980: 75) treated Gasowska's *Parchrosomus* as a synonym of *Phoxinus*, but without giving justification for this decision. Argument supporting Robins *et al.* rejection of this taxon is given above (p. 64).

### Species recognised as belonging to *Phoxinus*

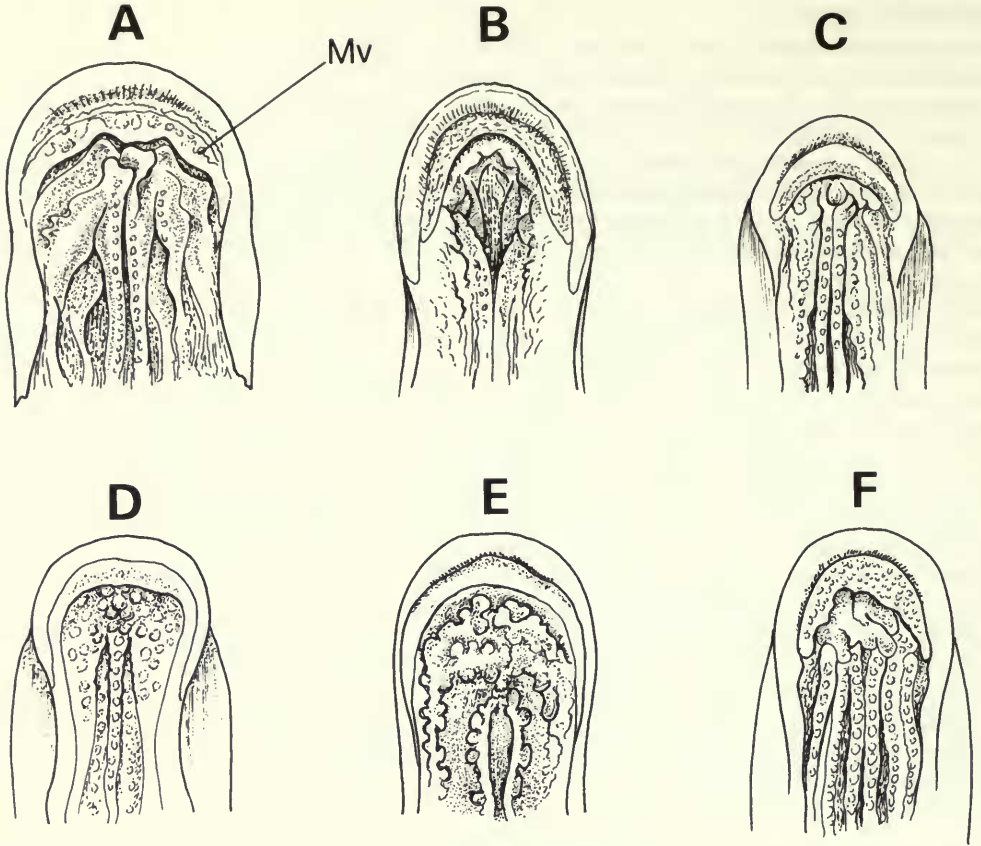
The following species are considered as belonging to the genus *Phoxinus*:

EURASIAN SPECIES: *Ph. brachyurus* Berg, 1912 (Ili basin); *Ph. phoxinus* (Linn., 1758), Europe (including the British Isles and Russia; see Berg, 1949 for distribution. *Ph. issykulensis* Berg, 1912. Lake Issyk-kul and drainage; *Ph. sedelnikowi* Berg, 1908. Basins of the Ili, Balkash and Issyk-kul.

Apart from *Phoxinus phoxinus* no specimens of the other three recognised Asian species have been available for examination and their inclusion is based solely on the characters given by Berg (1912; 1949), namely, the length of the jaw (in all species) and the naked abdomen (in *Ph. sedelnikowi*).

The central Asian species referred to *Phoxinus* by Berg (1912; 1932; 1949) *viz.* *poljakowi* and *czekanowskii*, should most probably be referred to the genus *Lagowskiella* (see above, p. 63). As *Ph. czekanowskii* is the type species of Dybowski's (1916) subgenus *Czekanowskiella*, that taxon is placed tentatively in the synonymy of *Lagowskiella* (p. 63).

Only a single specimen of *Ph. poljakowi* is available to me. It possesses a shallow lower jaw, attenuated operculum, somewhat divergent posterior infraorbitals, a large bucco-branchial aperture, and papillate gill-rakers. Similarly, *Ph. czekanowskii* has an attenuated opercular border and divergent infraorbitals, but the bucco-branchial opening is more restricted, as in *Phoxinus (sensu stricto)*; the specimens to hand are too poorly preserved to ascertain the morphology of the gill-raker membrane. No examples of the various *Ph. czekanowskii* subspecies recognised by Berg (1949) have been examined. The close resemblances between *Ph. poljakowi*, *Ph. czekanowskii* and *Lagowskiella lagowskii*, with the published descriptions of *Ph. dementjevi* Turdakov & Piskarev (1954) from the Chu River, Kazakhstan, and *Ph. grumi* Herzenstein (1889; in Berg, 1906) from Turfan Oasis, suggest that they all belong to *Lagowskiella*.



**Fig. 7** Buccal roof tissue in A, *Phoxinus phoxinus*, BMNH 1974. 8.6: 43–62, 70 mm SL; B, *Ph. neogaeus*, UMMZ 108044, 54 mm SL; C, *Ph. eos* UMMZ 185407, 51.5 mm SL (n.b. Maxillary valve is papillate over half its width); D, *Ph. erythrogaster*, UMMZ 144867, 40.5 mm SL; E, *Ph. cumberlandensis*, UMMZ 201152, 50 mm SL (n.b. *Ph. oreas* has a similar morphology); F, *Couesius plumbeus*, UMMZ 133303, 74.5 mm SL. Mv = maxillary valve.

**NEARCTIC SPECIES:** Mahy (1975) recognised *Ph. neogaeus*, *Ph. eos* and *Ph. oreas* as races of a single species, *Ph. erythrogaster*, although this is not generally accepted by North American workers; see for example, Lee *et al.* (1980). Legendre (1970) considered, on the basis of chromosome numbers, that *Clinostoma margarite* Cope, 1868 belonged to *Phoxinus*. Lee *et al.* (1980) refer *margarita* to the genus *Semotilus*, an action with which I concur. Joswiak *et al.* (1980) reviewed the karyotypes of *Phoxinus* species and suggested that populational differences were exhibited in chromosome number. However, the authors admit that pairing of homologous chromosomes is partially subjective and that a chromosome may be misclassified owing to differential arm contraction. Their conclusion is that chromosome analysis ‘... does not clarify affinities within the genus’. The relationships between nearctic species are discussed below (p. 70).

#### **Relationships and geographic distribution of *Phoxinus***

**Relationships:** The principal synapomorphy characterising *Phoxinus* species—the comb-like pectoral scales—occurs elsewhere only in the nearctic genus *Couesius*. As in *Ph. phoxinus*, the scales of *Couesius* have scalloped edges, and in ripe males cover an extensive area of the pre-pectoral region extending mesad to the midline (Fig. 2D). *Couesius* shares with *Phoxinus* species

a derived form of buccal roof tissue, one that is deeply furrowed and papillate, and a heavily papillose maxillary valve; see below and Fig. 7F.

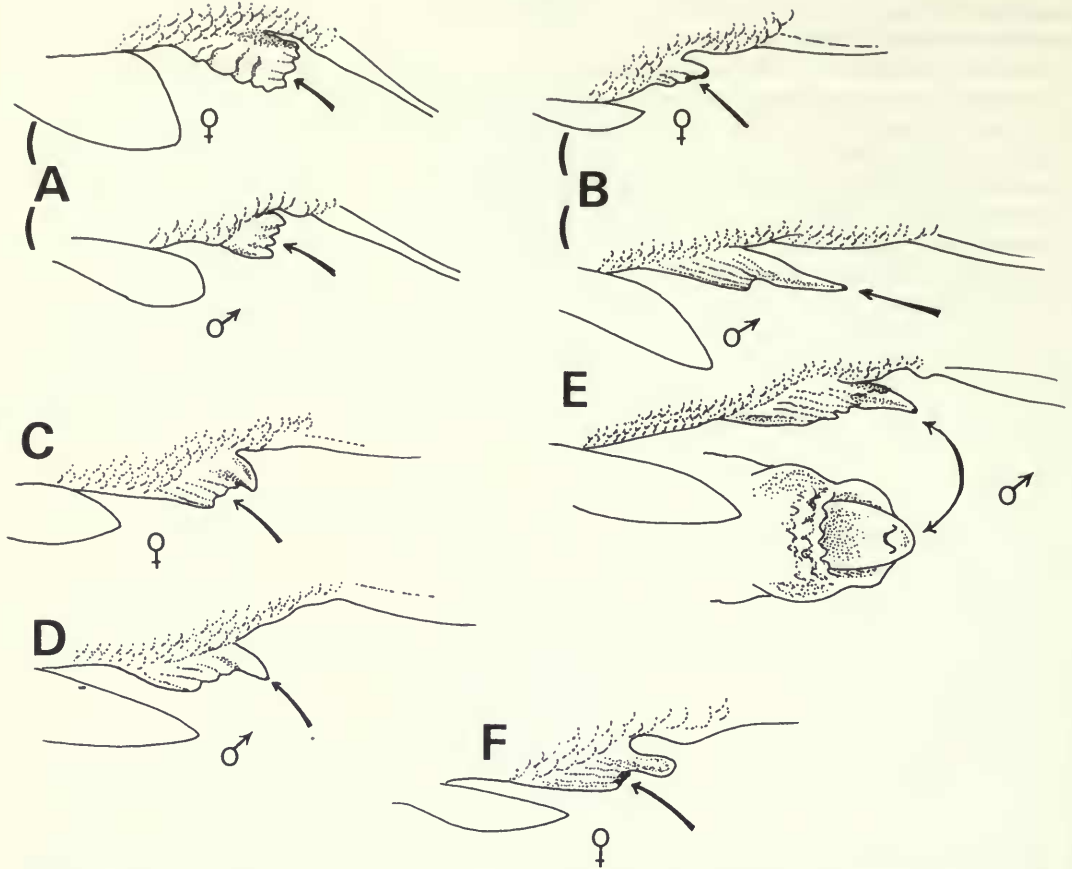
The comb-like breast scales in Eurasian *Phoxinus* have, for the most part, been overlooked. The otherwise comprehensive accounts of sexual dimorphism in *Phoxinus* by Frost (1943), Oliva (1953) and Lohinsky (1964) fail to note this character, but Gasowska (1979) used the feature to separate *Ph. phoxinus* from *Ph. percnurus* (referred here to *Eupallasella*; see p. 61). The presence of comb-like or tuberculate scales is well known amongst the nearctic *Phoxinus* species (see for example, Scott & Crossmann, 1973; Starnes & Starnes, 1978). In non-breeding male and female *Phoxinus*, belly scales are lacking and although there may be pre-pelvic scale patches they never meet in the midline. In the pre-pectoral area of non-breeding fishes, there are small tubercles (unculi of Roberts, 1982). There is a wide variation in the morphology of the breast 'scales' in *Phoxinus* species. Those in *Ph. erythrogaster* are smaller, having more the appearance of 'prickles' and are arranged in more regular rows than those of *Ph. phoxinus* (Fig. 2C), whereas those in *Ph. neogaeus* are cushion-like (Fig. 2B). In breeding males of all *Phoxinus* species a patch of tubercles is developed on the dorso-posterior corner of the operculum (Fig. 2C). In *Ph. phoxinus* there is an associated swelling of the opercular epithelium which forms a marked protuberance (see Lohinsky, 1964, fig. 2).

The development of the buccal roof tissue in *Phoxinus* and *Couesius* appears to be a derived feature. Although many cyprinid taxa have convoluted and furrowed mouth lining (e.g. *Barilius*) they lack the large 'tubercular' papillae (Fig. 7).

Osteologically, *Couesius* is very similar to *Phoxinus*; both taxa share a narrow ethmoid bloc, slender jaw bones and a spear-like coronomeckelian bone. *Couesius* differs from *Phoxinus* in its attenuate operculum, posteriorly extended cleithral lamina, belly completely covered with scales, and the presence of a posterior barbel. The barbel is unlike that of barbines, barbelled carps or of *Tinca*, and is a papillate appendage of the upper rectal tissue.

Although *Phoxinus* and *Couesius* may be regarded as sister groups, it is not possible to say, on the basis of known synapomorphies which is the more derived taxon. The relationships of the *Phoxinus*-*Couesius* lineage are also problematical. No synapomorphies have been identified that would denote sister-group relationship between this lineage and any of those taxa treated in this review. *Eupallasella* and *Rhynchocypris* have phoxinine-like features, particularly in having a small buccal-branchial aperture, small scales and pleated genital papilla; although it must be said that these features are mosaically distributed amongst cyprinid taxa and may, therefore be plesiomorphic. However, both genera share a mottled colour-pattern (Figs 5A-C) which is unusual in cyprinids, and may indicate their close relationship with one another. On the other hand, *Rhynchocypris* shares with *Lagowskiella* a derived form of male genital papilla whereby a conical projection carrying the spermatic duct to a terminal pore, extends beyond the anal orifice (Figs 8B; D). Females of both genera also possess a blind-ending conical fleshy projection (Fig. 8C). Two other taxa possess similar genital morphology; *Oreoleuciscus* and some species of Croatian '*Phoxinellus*' (Figs 8E; F). In these taxa, however, it is only the males of *Oreoleuciscus* and the females of '*Phoxinellus*' that share the derived conditions of their counterparts in *Rhynchocypris* and *Lagowskiella*. *Oreoleuciscus* females and '*Phoxinellus*' males lack the genital processes. On the basis of derived osteological and other characters it seems likely that *Lagowskiella* is related to the aspinine assemblage (see p. 63). *Rhynchocypris*, on the other hand, may have a closer affinity to the Croatian '*Phoxinellus*' and the phoxinines (*Phoxinus* + *Couesius*).

A more precise theory of relationships is hampered by inadequate knowledge of *Phoxinellus* species. Trewavas (1971) referred to both the alpha and the beta level taxonomic problems associated with *Phoxinellus*. The situation was not improved, and indeed was marred, by Karaman's (1972) revision of the genus. Karaman included in *Phoxinellus* several species which had originally been assigned to various rutiline and leuciscine genera; it is clear, however, that he is in error, as the following discussion indicates. Some Croatian species of *Phoxinellus* (*sensu* Karaman), referred to above and formerly assigned to *Paraphoxinus* (*pstrossi*, *ghetaldii*, *croaticus* and *metohiensis*) are not members of that genus and represent a distinct taxon (or taxa). *Phoxinellus* (*sensu stricto*) includes those species distributed throughout the Levant (*adpersus*, *zeregi*) and possibly the north African species *chaignoni*, *callensis* and *guichenoti*, which have no



**Fig. 8** Genital papillae shown in lateral views of A, *Phoxinus phoxinus*, ripe female, 72.5 mm SL and ripe male, 60 mm SL; B, *Lagowskiella lagowskii*, female, 70 mm SL and male, 70 mm SL; C, *Rhynchocypris oxycephalus*, ripe female, 92.5 mm SL; D, *Rhynchocypris steindachneri*, male, 47 mm SL; E, *Oreoleuciscus humilis*, male, 76.5 mm SL, also shown in ventral view; F, '*Phoxinellus*' *pstrossi*, ripe female, 87 mm SL. Arrows indicate position of genital orifice.

close relationship with either the Croatian '*Phoxinellus*' or with *Phoxinus*, but belong to a rutiline assemblage. The Croatian '*Phoxinellus*' share with *Phoxinus* absence of scales midventrally, and with *Rhynchocypris* an attenuated operculum, genital morphology, mottled colour pattern and, in some species, a fleshy rostral process (see Fig. 4). The relationships of the phoxinine lineage, *Phoxinus* + *Couesius* can only be established when a more complete study of the anatomy and taxonomy of the Croatian '*Phoxinellus*', *Rhynchocypris* and *Eupallasella* species have been undertaken.

**Geographic distribution:** Despite what may appear to be radical changes in the synonymy of *Phoxinus*, the distribution pattern is little different from that mapped by Bănărescu (1964, fig. 142). The only change is that the range given by Bănărescu for *Phoxinus phoxinus* now represents the range of the genus in Eurasia.

Regarding the nearctic species, both Legendre (1970) and Mahy (1975) account for the present distributional pattern by various post-glacial migrations and hybridisations. Mahy (1975) recognises *Ph. erythrogaster* as the plesiomorphic species (Mahy's 'primordial race'), and as having dispersed from its Mississippian refuge, whilst *Ph. neogaeus* dispersed over a more northerly area from its Missourian refuge. This of course presupposes that two taxa were specifically distinct

prior to glaciation. If, on the other hand, *Ph. neogaeus* is considered to be the plesiomorphic North American species (as suggested by its broader ethmoid bloc and larger circumorbital bones), then its formerly widespread distribution can be seen, through the intervention of glacial episodes, to result in a disjunct pattern, the fragmented elements being represented by the derived extant species (or races, as recognised by Mahy).

Patterson (1981: 266) notes that theories of postglacial dispersal have been dominant in considering the distribution of North American fishes. It may be that the effects of glaciation were not so profound as to have extinguished the majority of species. Fewer propositions are necessary to argue that *Phoxinus* was widely dispersed across Asia and North America prior to glaciation than to suppose its subsequent dispersal. Mahy (1975) contended that *Ph. phoxinus* was more closely related to *Ph. neogaeus* than to the other North American species. This hypothesis has yet to be tested by cladistic analysis, the results of which will also provide a framework for testing vicariance as opposed to dispersal hypotheses of the species' distribution.

### List of taxonomic changes

The following binominal combinations are those used by previous workers and those recognised in this study:

Species and author	Former generic assignment	Combination recognised in this paper
<i>atrilatus</i> Jordan & Thompson, 1914	<i>Pseudaspius</i>	<i>Rhynchocypris steindachneri</i>
<i>bergi</i> Jordan & Metz, 1913	<i>Pseudaspius</i>	<i>Lagowskiella lagowskii</i>
<i>brachyurus</i> Berg, 1912	<i>Phoxinus</i>	No change
<i>brandti</i> Dybowski, 1872	<i>Telestes</i>	<i>Tribolodon brandti</i>
<i>brandti</i> (non Dybowski) Fowler, 1899; 1924	<i>Leuciscus</i>	<i>Rhynchocypris oxycephalus</i>
<i>chorensis</i> (subspecies of <i>lagowskii</i> ) Rendahl, 1928	<i>Phoxinus</i>	<i>Rhynchocypris oxycephalus</i>
<i>costatus</i> Fowler, 1899	<i>Leuciscus</i>	<i>Rhynchocypris costatus</i>
<i>cumberlandensis</i> Starnes & Starnes, 1978	<i>Phoxinus</i>	No change
<i>czekanowskii</i> Dybowski, 1869	<i>Phoxinus</i>	? <i>Lagowskiella czekanowskii</i>
<i>dementjevi</i> Turdakov & Piskarev, 1954	<i>Phoxinus</i>	? <i>Lagowskiella dementjevi</i>
<i>dorobae</i> Ishikawa, 1904	<i>Leuciscus</i>	<i>Rhynchocypris steindachneri</i>
<i>eos</i> Cope, 1862	<i>Chrosomus</i>	<i>Phoxinus eos</i>
<i>erythrogaster</i> Rafinesque, 1820	<i>Chrosomus</i>	<i>Phoxinus erythrogaster</i>
<i>grumi</i> Herzenstein, 1889	<i>Phoxinus</i>	? <i>Lagowskiella grumi</i>
<i>issykkulensis</i> Berg, 1912	<i>Phoxinus</i>	No change
<i>jouyi</i> Jordan & Snyder, 1900	<i>Leuciscus</i>	<i>Tribolodon jouyi</i>
<i>jouyi</i> , Okada, 1960	<i>Moroco</i>	<i>Tribolodon jouyi</i>
<i>lagowskii</i> Dybowski, 1869	<i>Phoxinus</i>	<i>Lagowskiella lagowskii</i>
<i>lagowskii</i> , Fowler, 1924	<i>Phoxinus</i>	<i>Rhynchocypris costatus</i>
<i>lagowskii</i> , Mori, 1934	<i>Phoxinus</i>	<i>Rhynchocypris costatus</i>
<i>modestus</i> Jordan & Metz, 1913	<i>Pseudaspius</i>	<i>Rhynchocypris oxycephalus</i>
<i>neogaeus</i> Cope, 1868	<i>Phoxinus</i>	No change
<i>oreas</i> Cope, 1868	<i>Chrosomus</i>	<i>Phoxinus oreas</i>
<i>oxycephalus</i> Sauvage & Dabry, 1874	<i>Pseudophoxinus</i>	<i>Rhynchocypris oxycephalus</i>
<i>oxycephalus</i> (subspecies of <i>lagowskii</i> ) Berg, 1912; 1949	<i>Phoxinus</i>	<i>Rhynchocypris oxycephalus</i>
<i>oxycephalus</i> (subspecies of <i>lagowskii</i> ) Dulceit, 1927	<i>Phoxinus</i>	? <i>Rhynchocypris costatus</i>
<i>oxycephalus</i> , Mori, 1930	<i>Phoxinus</i>	<i>Rhynchocypris oxycephalus</i>
<i>oxycephalus</i> , Mori, 1934	<i>Phoxinus</i>	<i>Rhynchocypris costatus</i>
<i>percnurus</i> Pallas, 1811	<i>Phoxinus</i>	<i>Eupallasella percnurus</i>
<i>percnurus</i> , Gasowska, 1979	<i>Parchrosomus</i>	<i>Eupallasella percnurus</i>
<i>phoxinus</i> Linnaeus, 1758	<i>Phoxinus</i>	<i>Phoxinus phoxinus</i>
<i>poljakowi</i> Kessler, 1879	<i>Phoxinus</i>	? <i>Lagowskiella poljakowi</i>

<i>sachalinensis</i> (subspecies of <i>percunurus</i> ) Berg, 1906	<i>Phoxinus</i>	<i>Rhynchocypris oxycephalus</i>
<i>sedelnikowi</i> Berg, 1908	<i>Phoxinus</i>	No change
<i>semotilus</i> Jordan & Starks, 1905	<i>Richardsonius</i>	? <i>Phoxinus semotilus</i>
<i>semotilus</i> , Jordan & Hubbs, 1925	<i>Acahara</i>	? <i>Phoxinus semotilus</i>
<i>septentrionalis</i> (subspecies of <i>variegatus</i> )		
Mori, 1930	<i>Moroco</i>	<i>Rhynchocypris oxycephalus</i>
<i>steindachneri</i> Sauvage, 1883	<i>Phoxinus</i>	<i>Rhynchocypris steindachneri</i>
<i>steindachneri</i> , Jordan & Snyder, 1901	<i>Leuciscus</i>	<i>Rhynchocypris steindachneri</i>
<i>steindachneri</i> , Jordan, Tanaka & Snyder, 1913	<i>Hemitremia</i>	<i>Rhynchocypris steindachneri</i>
<i>steindachneri</i> , Jordan & Hubbs, 1925	<i>Moroco</i>	<i>Rhynchocypris steindachneri</i>
<i>steindachneri</i> , Okada, 1960	<i>Moroco</i>	<i>Rhynchocypris steindachneri</i>
<i>variegata</i> Günther, 1889	<i>Rhynchocypris</i>	<i>Rhynchocypris oxycephalus</i>
<i>variegatus</i> , Mori, 1930	<i>Moroco</i>	<i>Rhynchocypris oxycephalus</i>
<i>variegatus</i> (subspecies of <i>lagowskii</i> ) Berg, 1932	<i>Phoxinus</i>	<i>Rhynchocypris oxycephalus</i>
<i>yamamotis</i> Jordan & Hubbs, 1925	<i>Moroco</i>	<i>Rhynchocypris steindachneri</i>

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